



Merilaita, S., Scott-Samuel, N., & Cuthill, I. (2017). How camouflage works. *Philosophical Transactions B: Biological Sciences*, 372, 20160341. [20160341]. <https://doi.org/10.1098/rstb.2016.0341>

Peer reviewed version

Link to published version (if available):
[10.1098/rstb.2016.0341](https://doi.org/10.1098/rstb.2016.0341)

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How camouflage works

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Keywords: defensive coloration, signal-to-noise ratio, crypsis, visual search, animal coloration

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Summary

For camouflage to succeed, an individual has to pass undetected, unrecognized or untargeted, and so it is the processing of visual information that needs to be deceived. Camouflage is therefore an adaptation to the perception and cognitive mechanisms of another animal. Although this has been acknowledged for a long time, there has been no unitary account of the link between visual perception and camouflage. Viewing camouflage as a suite of adaptations to reduce the signal-to-noise ratio provides the necessary common framework. We review the main processes in visual perception and how animal camouflage exploits these. We connect the function of established camouflage mechanisms to the analysis of primitive features, edges, surfaces, characteristic features and objects (a standard hierarchy of processing in vision science). Compared to the commonly used research approach based on established camouflage mechanisms, we argue that our approach based on perceptual processes targeted by camouflage has several important benefits: specifically, it enables the formulation of more precise hypotheses and addresses questions that cannot even be identified when investigating camouflage only through the classic approach based on the patterns themselves. It also promotes a shift from the appearance to the mechanistic function of animal coloration.

Introduction

In zoology, body colours and patterns and other morphological adaptations that decrease the probability that an animal will be detected or recognised are called camouflage. Animal camouflage, including cryptic coloration (i.e., coloration that decreases the risk of being detected [1]), has been studied for over a century. The pioneers of the field proposed various ways that colours and patterns could be used to improve camouflage. What are now usually called background matching, disruptive coloration, masquerade, self-shadow concealment, distractive marks and motion dazzle, are concepts that are based particularly on the writings of Thayer [2] and Cott [3], and research on animal camouflage during recent decades has mainly focussed on providing evidence for, and conceptual development of, these principles.

Undoubtedly the classic works by Thayer [2] and Cott [3] have provided an invaluable source of ideas and hypotheses to be tested. Yet it is important to remember that their work, reflecting the approaches used

and knowledge available in their times, has limitations because it was based on their subjective impressions of animal coloration and application of ideas about optics [4].

An analysis of the physical properties of a colour pattern (either in terms of materials or light reflected and entering the eye) would provide an approach free of subjectivity, but can never be sufficient to understand camouflage, or indeed animal signals. This is because the effects generated by animal colours and patterns are, in addition to optical factors and stimulation of photoreceptors, influenced by processing of visual information that reaches the eye of the viewer. When considering these visual and cognitive processes, we would expect that protective coloration has been selected to exploit the weak spots in the processing to manipulate the viewer. That these processes have limitations is demonstrated by the massive loss of information that takes place when processing a visual scene. The light reaching the retina is a continuous distribution in terms of wavelength, time and space. A retina reduces this to a very few wavebands (for humans three – long, medium and short – and for most animals between two and four [5]) at a discrete sampling frequency in space and time. For example, the human retina processes about 10^6 bits per second [6], but only 1% of this information is transmitted down the optic nerve. However, detailed serial processing of the focus of visual attention only occurs at about 100 bits/s, so the scale of information loss is about 10:1 and that at the so-called “attentional bottleneck” is 10:1 [7]. Despite data compression, sparse efficient coding, and redundancy in natural scenes, information is lost. The lesson is that any system that takes shortcuts in processing information can be exploited. This is what camouflage does. Thus studying only photon flux and ignoring perception cannot lead us to an understanding of how camouflage works.

Here we assess the function of camouflage coloration by reviewing the main stages in the hierarchical process of visual perception, which camouflage targets. Corresponding to the principles of visual perception of objects, we argue that camouflage coloration can be used to reduce the salience of the (1) primitive features, (2) surfaces, (3) edges, (4) characteristic compound features (cf. parts of body) and (5) object (i.e. whole animal). Beyond these morphological properties of an animal, we also address (6) camouflage of motion and the confusion effect and (7) the effect of visual background complexity on detection. We connect the established camouflage mechanisms to these processes. We assert that approaching camouflage through the processes it targets enables formulation of more precise hypotheses and the addressing of questions that cannot even be identified when investigating camouflage only through the classic approach based on the patterns themselves. We also propose that for understanding various mechanisms of camouflage the concept of signal-to-noise ratio (SNR) provides a useful tool, and so we identify the signal and the noise relevant to each camouflage mechanism.

Signal-to-noise ratio

SNR compares the amount of useful information to the amount of irrelevant or false information. We focus on how camouflage acts to minimise the SNR at different stages in visual processing (Table 1). The target, or some diagnostic aspect of the target, is the signal, and all factors that interfere with extraction and identification of that signal constitute noise. Although it is the SNR that has the central role in signal processing theory, its value is obviously affected by differences in signal, noise, or both. Background matching camouflage minimises signal, disruptive coloration minimises (true) edge signals but also creates noise through false edges. For a moving target, the SNR could be decreased by associating with a large number of conspecifics (increased noise via the confusion effect), or by trying to minimise one’s own movement signal (via stalking, or eliminating motion across an observer’s retina), or some combination of both. For a prey item’s diagnostic features, like eyes, noise can be added to that signal: coincident disruption, false features (e.g. eyespots), eye stripes and distraction markings. Finally, in the case of mimicry and masquerade, the signal is not diminished; in this case there is increased noise arising from a salient but false signal from the prey item.

Visual perception

While it is convenient to conceive of vision as a sequence of information processing steps from photoreceptor to feature detection to object recognition to mental representation, with perception following sensation and ‘cognition’ following perception, this can be misleading. Certainly some visually guided behaviours are driven fairly directly by near-receptor processing (e.g. many escape reflexes [8]), but some tasks involving object recognition cannot be understood solely in terms of bottom-up flow of information. Top-down factors can introduce biases at multiple steps in the pathway, with expectations and goals affecting every step, from where your eyes move to stored memories [9]. Vision therefore typically involves a mixture of bottom-up and top-down processes. It can be thought of as an iterative process of evaluating competing hypotheses about the content of a visual scene [10], based on both current receptor input and priors, either deeply entrenched through evolution or early life, or flexibly updated through recent experience. Camouflage manipulates the visual information available to the viewer in the light of not only the current visual scene (‘the background’) but those priors upon which that viewer will make judgements such as ‘present or absent’, ‘edible or inedible’, ‘attack or ignore’.

Primitive features

The first post-receptor processing of visual information consists of the detection of differences in neural firing at particular spatial or temporal scales. These may correspond to differences in the intensity of incident light or the distribution of wavelengths. Dependent upon the shape, size, orientation and temporal resolution of the neuron’s receptive field, a primitive feature is encoded corresponding to a point or line, of a given size, orientation and magnitude, at a particular time. From these simple features in so-called early vision, the scene is partitioned into surfaces and edges. The two are intimately related, because a surface is bounded by an edge and that edge is recognised by an abrupt change in surface properties; but because of differences in processing it is convenient to consider the two in turn.

The encoding of simple features in early vision has two key roles. One is to provide the raw material for assembly into contours, surfaces, compound features and objects by downstream regions of the brain. The second is as a saliency map to guide more detailed inspection (e.g. [11]). High saliency, here, is defined as any feature (chromatic, textural, temporal) that stands out from the overall distribution. In primates, high saliency drives a visual saccade to bring the fovea, which has high spatial and chromatic resolution, to bear on this region of the visual scene of potential interest. In animals that are less reliant on eye movements, allocating visual attention by movement of the head or body is still an important part of analysing the visual scene [12–14]. Therefore the first and most basic role of background matching camouflage is to be coloured such that no features are salient and so detailed inspection does not occur. The signal here is the set of primitive features of the target, the noise those of the background.

Surfaces

A common route to camouflage is to have a surface that mimics the appearance of the background, usually called background matching (in older texts, “generalised resemblance” [1] or “background picturing” [2]). Such resemblance corresponds to decreased SNR (row 1, Table 1). The animal’s surface need not reproduce the exact effects of the background on incident light: the relevant match is only that of the spatial patterns perceived by the viewer at the distances and viewing angles that are relevant to avoiding detection [e.g. 15, 16, 17].

Some backgrounds are relatively homogeneous and can be described as a single surface. Other backgrounds may comprise multiple surfaces (e.g. a forest floor with different coloured leaves, stones and

earth). In the context of camouflage, one critical factor is the heterogeneity at the spatial scale of the animal [15, 16]. Imagine a background that is a repeating checkerboard extending in all directions. If an animal is much smaller than a single square then the prey should either be black or white. Alternatively, a prey item that is much larger than a square should bear a checkerboard pattern. This logic, considering camouflage as a sample of the background at the spatial scale of the animal, has a long history [2] and has been an influential concept [18, 19]. But if the animal's movement range covers several, different squares or the background is continuously variable, what is the best sample to be? This is a research area deserving more attention. In any one location, of course, gene flow may mean that not all observed phenotypes are at the local optimum [20]. Beyond this, there are two major empirical problems facing researchers. First, if the optimum is a compromise across multiple backgrounds [21, 22], not only do the candidate backgrounds have to be identified and the frequency of occurrence of the animal on them quantified, but also the likelihood of their being viewed there. The second difficulty is quantifying the match of animal to background. This must be done with respect to the visual system of the evolutionarily relevant viewers [15, 23] under the appropriate illumination and viewing distance/direction [15, 24]. While suitable data and models now exist for many species' colour perception [e.g. 25, 26], there is no equivalent 'texture space' into which we can map natural textures and so quantify their difference. There is no universally accepted theory of how humans, far less other animals, perceive and discriminate textures, although there is good evidence for how some lower-level properties of textures (spatial frequencies, phases and orientations) are detected and encoded in low-level vision. There are also viable algorithms in machine vision that give clues about how nervous systems might represent textures [e.g. 27], and some have been applied to animal colour patterns [28-30, 31], but currently we have no real idea of how valid these are. Finally, factors other than background matching also influence selection on coloration [32-34].

Edges

That edges have a key role in vision is evident from the fact that a pencil sketch, using only outlines, is sufficient for us to identify more or less any object. Edges help identify where one object's surface stops and another starts, so are important in object detection, and a coherent bounding edge (an outline) is a primary cue to identity. If an animal matches the background perfectly then there is no perceptible edge (row 3, Table 1). However, slight misalignments between animal and background, what we would now describe as differences in phase or orientation of the texture, can create edge information, just as can more obvious differences in surface properties, such as lightness, colour or spatial frequency. Thayer [2] recognized this and proposed a set of variously complementary or alternative mechanisms to background matching, under the heading 'ruptive coloration'. The most widely accepted of these is disruptive coloration, the strategic placement of contrasting colours that break up shape and form [3, 35]. Disruptive coloration may exploit several perceptual mechanisms, but the simplest (in as far as involving only low-level vision) is through creating false edges [29, 36] (rows 4, 5, Table 1). If some colour patches at the body's edge match the background closely (differential blending [3]) and others contrast strongly with these, then the between-patch edge signal is strong and the true body outline has weak coherence. Here the signal is the true edge and the noise false edges. Cott [3] argued that the internal contrast should be maximal, even if this means that these patches do not match the background. There is some evidence that placing such, otherwise conspicuous, patches at the body's edge is less of a cost than placing them elsewhere [37, 38], but also evidence that disruptive placement of colour patches that are contrasting, but nevertheless found in the background, provides better concealment [38, 39].

High contrast markings can potentially interfere with (true) edge detection in ways other than representing a strong, albeit false, edge signal. Neurons with receptive fields including such markings will show reduced sensitivity to nearby weak stimuli, through lateral inhibition (row 6, Table 1). Thus strong false edges can mask nearby weak true edges. There is certainly evidence that high contrast disruptive-type patterns can reduce prey detection by birds even when they do not overlap a target's outline [40]. However, there are no experiments that isolate the mechanism as lateral inhibition and there are other

potential explanations (discussed below) that, unlike those discussed so far, involve interference with attention.

Characteristic compound features

Many animals have salient or prominent body parts that can facilitate detection, recognition or targeting. Well-known examples are the vertebrate eye or the long hind legs of grasshoppers and anurans [3]. Interestingly, because such body parts are often viewed against the surrounding parts of the body, the organism in question has full genetic and developmental control over both the feature to be concealed and its immediate visual background, and therefore concealment of such features could provide opportunities for evolutionary perfection of camouflage: they could also provide researchers with opportunities to test ideas about camouflage, without the interference of background variation. This requires that the effect of developmental correlation in coloration between different body parts that are covered by continuous cuticular tissue is taken into account, but when the feature and its surrounding are histologically different, such as the eye and the skin, scales, feather or fur surrounding it, it may be easy to identify selection for concealment of a feature.

Coincident disruptive coloration (row 8, Table 1) may provide a means to camouflage morphological features that could reveal the presence or identity of an animal [3]. Strategic placement of patches of separate colours with a sharp contrast and similar colours may generate false discontinuity within a surface, false continuity between adjacent, discontinuous surfaces and false edges that extend across adjacent, discontinuous surfaces. This way a coordinated organization of patterning on the feature and the adjacent area may generate a coincident disruptive effect. Coincident edges (e.g. on the torso and an extremity overlapping it) generated by two contrasting colours and when the patterns are in phase do indeed increase camouflage through concealment of a prominent feature [41]. As with simple disruptive coloration, the false edges constitute noise to mask the signal of the body part's true outline.

A single mark, such as an eye stripe (a facial stripe running across the eye), can also be used to generate a coincident disruptive effect (row 8, Table 1). Many fish sporting an eye stripe also have a potentially divertive eyespot (a mark that consists of more or less concentric and circular patches of contrasting colours, like the vertebrate eye) and thus, for the diversion to work, the eyespot needs to beat the actual eye in competition for the attention of a striking predator (row 9, Table 1). Kjernsmo et al. [42] showed that attacking fish direct their strikes towards the intact eyelike mark on an artificial prey and away from the disrupted eyelike mark; an eye stripe can effectively reduce SNR by providing a more salient feature than the true eye.

The combined effect of an eye stripe and an eyespot to decrease the relative salience of the eye reveals an additional way to camouflage exposing features. Stimuli in the visual field compete for visual attention of the observer. Therefore, a more salient feature could divert the attention of a viewer [43] (row 10, Table 1). In addition to attentional processes of high-level vision, lateral masking (i.e., impaired perception of a stimulus when other stimuli are nearby) might also be exploited in the concealment of features [44].

One adaptive function suggested for eyespots is diversion ("deflection") of attacking predators, and recent experiments have shown that eyespots can be used to manipulate where predators aim their strikes [e.g. 42, 45]. For predators, the location of the head area of a prey may indicate its escape direction or a vulnerable area. Therefore distorting that information can increase the prey's chance of surviving an encounter with a predator. In vertebrate taxa, such as fishes, eye mimicry may also be involved in the divertive effect of eyespots, but due to the non-eyespot-like appearance their eyes, this is probably not the case in invertebrates.

The proposed perceptual mechanisms targeted by distractive and divertive marks are the same, but while divertive marks manipulate an attacking predator's perception to influence the direction of the strike, distractive marks improve the camouflage of an animal by impeding the detection or recognition of its characteristic shape [46].

Generally, because divertive and distractive effects are based on making perception of one feature difficult by increasing the salience of other features (decreasing SNR by increasing noise; rows 7, 8, 9, 10, Table 1), it is not the salience of a divertive or distractive mark as such but the effect of the mark on how the viewer perceives and responds to it that determines whether the mark is effective [47]. An interesting question is how the visual properties of the environment (e.g. salient features of the background) influence the costs and benefits of divertive and distractive marks (see later: Background Complexity).

Objects

Although simple geometric shapes are defined by a single bounding edge and surface, most biologically relevant objects, and certainly most prey items, comprise a characteristic arrangement of multiple surfaces. How multiple components of an object come to form a single percept, the process of 'feature binding', is a central problem in both biological and machine vision. Furthermore, most organisms have a three-dimensional form that can be viewed, and so must be recognised, from multiple perspectives. Therefore the fundamental higher-level task of vision is to assemble features that 'belong together' into discrete objects and to reconstruct 3D shape from a 2D retinal projection. Although disruptive coloration can, through the use of false edges, interfere with detection of (true) surfaces and disguise single body features that might in themselves reveal an animal's presence (both discussed earlier), it has long been proposed to interfere with object recognition [2, 3, 35, 36]. It is thought to do so by acting against the mechanisms of feature binding [48] (row 11, Table 1). This is why, like illusions, camouflage can help us to understand the mechanisms of visual perception [49]. Indeed, the influential Gestalt school of psychology, which developed the first coherent principles of object perception at the start of the 20th century, often used animal camouflage to illustrate their theories [4]. Although Gestalt approaches to vision have been largely superseded by computational neuroscience, many of the principles of the former are nonetheless embodied in the latter; they must be, as the Gestalt principles were established to explain, or at the very least describe, empirical findings.

Disruptive coloration can be thought of as 'anti-Gestalt'. Thus Gestalt principles would group together features that are similar, whereas disruptive camouflage features sharp contrasts in colour between adjacent patches on the animal, with some or all patches matching different parts of the background more closely than they match each other. In this way, colour patches (surfaces) segregate with different surfaces in the background rather than together as a potentially recognisable object. Disguising true edges and creating false edges, both common components of disruptive camouflage, act against Gestalt principles of continuity and closure of boundaries. Symmetry is another Gestalt principle that is detrimental to crypsis [50, 51], so it remains somewhat of a paradox that so many camouflaged animals are nonetheless symmetrical. Developmental constraints that tie surface coloration to an underlying symmetrical body plan are likely to play a role. However it is also the case that some symmetrical patterns are more cryptic than others [50] and it remains unexplored whether animals employ a subset of patterns that are less negatively influenced by symmetry than others. There are also behavioural means of disguising symmetry or rendering it less salient [see discussion in 52].

Feature binding can be influenced by top-down processes, namely an expectation, through learning, for a conjunction of specific features that are diagnostic of a target. Biologists call this a search image [53], a relatively short-term perceptual filter requiring selective attention [54]. An important consequence of this requirement is that search is slow and inefficient, and improvements in detection of one prey type (or rather, conjunction of features) is accompanied by reduced detection success for others [55, 56]. Search image formation can result in frequency-dependent predation that selects for prey polymorphism, as

shown elegantly by Bond and Kamil [57]. Prey polymorphism, on the other hand, makes the search task more demanding [58].

Once feature binding has occurred and the target animal has been segmented visually from its background, other camouflage mechanisms can defeat object recognition. One is to disguise shape so that the form is unrecognisable, the other is to resemble an irrelevant object; the latter is the form of mimicry most commonly called masquerade [59] (row 12, Table 1). Camouflage through posture has been investigated in the context of orienting correctly to textured backgrounds [e.g. 60], and mimicry of specific objects (see below), but there has been little empirical work on the potential benefit of being an unrecognisable form through contortions of body shape, as seen in cephalopods.

Looking like the background and looking like an object within the background would seem superficially similar. The logical distinction between masquerade and background matching is that the former can, in principle, be effective even if the animal is isolated and in plain sight: it is detected but not recognised. In practice, the effectiveness of masquerade depends on predators having learnt that the object being mimicked is irrelevant, and it is more effective when mimicked objects are present [61]. Therefore masquerading prey may often also benefit from background matching: a stick insect is cryptic because it both looks like a stick and blends with sticks. Some animals, most spectacularly octopuses, can mimic both different backgrounds and multiple objects [e.g. 62, 63], and there is potentially a benefit both of masquerade and the fact that the animal is encountered in multiple forms, making its characteristic features harder to learn. To our knowledge, this has not been investigated.

In the interests of convenience, the majority of experiments on camouflage, and visual search more generally, consider two-dimensional objects in a single depth plane. However most biologically relevant objects are 3D, and many interactions with them involve depth judgements. The reconstruction of depth from the 2D retinal images is therefore a key stage in vision, both for assessment of object shape and the relationships between objects in space. One important cue comes from the patterns of shading arising from light coming from above. One of Abbott Thayer's sharpest insights was that even if an animal colour-matches the background perfectly, it could be revealed by these shape-from-shading cues. Thus he argued that 'countershading', darker pigmentation on the side facing the illumination (usually the animal's back), had evolved to minimise shape-from-shading cues by nullifying the gradient of illumination [2, 64] (row 2, Table 1).

Although countershading is common and taxonomically widespread, there are other good reasons to be more densely pigmented on the side facing the sun [e.g. protection from ultraviolet illumination; 34, 65]. Furthermore, the density and gradient of pigmentation needs to match the lighting conditions (e.g. direct or diffuse illumination) and the animal must orient appropriately, for the strategy to be effective [33, 66]. However, cross-species comparisons suggest that the observed pattern of countershading does match the prevailing lighting conditions, as one would predict for countershading [67, 68]. Also, predation experiments with artificial caterpillars show that countershaded prey have reduced attack rates by birds [69].

Motion, individuation and the confusion effect

Motion breaks camouflage: humans and other species are exquisitely sensitive to movement. Given the necessity to forage, for example, this presents a problem for prey items. There are some behavioural solutions: to attempt background matching in the temporal domain, by adapting one's own motion to be similar to the environment [63], or to adapt one's movement to minimise any motion signal to a potential predator [70] (row 13, Table 1).

If these sorts of strategies cannot be implemented, then dazzle camouflage [2] - high contrast geometric surface patterns - has been hypothesised to disrupt a predator's ability to intercept a target, either via distortion of speed, trajectory, or both (i.e. it generates noise in the velocity signal) (rows 14, 15, Table 1). Despite its widespread use on shipping in the First World War, and many anecdotal accounts of its efficacy [71] it is only recently that controlled data have been gathered to investigate whether the technique actually works. The evidence is mixed, with multiple groups reporting different and sometimes contradictory effects of dazzle camouflage [72-76]. Nevertheless, it appears that surface colouration can influence perceived velocity in multiple ways, and this is a promising area of future research.

Recent evidence indicates that colouration has some effect on predation success for multiple moving targets [73, 77-79], possibly reflecting an interaction between colouration and the confusion effect. Most predators must individuate a single target when attacking a group. The confusion effect is taken to reflect the overloading of predator cognition at multiple levels [80] (row 16, Table 1), and scales with the number or possibly density of prey items [81, 82]. The unpredictability of prey motion might reasonably be expected to interact with the confusion effect, but the evidence so far is mixed [82, 83].

The idea that increasing numbers of items can interfere with cognitive processing has an extensive literature in the domain of human perceptual psychology (for a review see [84]) under the umbrella term "visual search", and there is clearly room for cross fertilisation of ideas here [85]. Within the animal literature, the different approaches - natural systems [e.g. 86], lab based animal experiments (e.g. [81]), computational modelling (e.g. [80]) and human predator manipulations (e.g. [78]) - have yet to be unified and combined effectively. One promising avenue would be to use movement data from recordings of species in the wild (e.g. [87]) to drive the more controllable experiments that can be run on human observers.

Background complexity

The environment of the concealed animal is typically considered as the background into which the animal needs to blend to decrease its risk of being detected. Psychological experiments have shown that not only the similarity between the targets and non-targets, but also the properties of the non-targets per se, such as their dissimilarity, influence search efficiency [88]. Considering SNR, this corresponds to change in the level of various types of noise interfering with different perceptual processes. Accordingly, predation experiments have confirmed that when the degree of background matching of the prey is kept constant, increasing the geometric diversity, density, complexity of shape and luminance range of the geometric elements constituting the visual background have a negative effect on prey detection rate (e.g. [46, 89]). Also, a recent field study indicates that an increase in the textural complexity of the background within a natural range of variation decreases the risk of prey being detected [90]. In other words, not only animal camouflage, but also the visual properties of the background influence the risk of the animal being detected. This has behavioural [91] and evolutionary [92] implications that have not yet been fully explored.

Conclusions

We have shown that the function of established camouflage mechanisms can be characterised as interference with the perception of primitive features, edges, surfaces, characteristic features or objects: in other words, disruption at different hierarchical levels of the organisation of visual perception. Approaching camouflage through the perceptual processes it targets provides several benefits compared to the classic approach based on patterns themselves. Overall it promotes a shift of focus from appearance towards the understanding of mechanistic function of animal coloration. It uncovers questions that cannot even be identified when investigating camouflage only through an approach based on the patterns

themselves. In addition, it enables formulation of more precise hypotheses. We think that a particularly helpful tool for this point is the concept of SNR. Camouflage acts to minimise the SNR at different stages in visual processing, and application of SNR requires identification of what constitutes the signal and noise through the targeted processes. The strength of the SNR approach is that it provides a common language with which to discuss different types of camouflage. Using an SNR framework allows similarities (and differences) across the various camouflage strategies to be highlighted. In all cases, as we have emphasised throughout, one must understand how information is processed in order to understand how the varied mechanisms of camouflage function.

Additional Information

Acknowledgments

We thank the Wissenschaftskolleg zu Berlin for funding our three-person brain-storming session that gave rise to this manuscript and for the Animal Coloration workshop that was the launch pad for the volume. Thanks also to Tim Caro for encouraging us to write this article.

Authors' Contributions

All authors contributed equally to all aspects of this paper.

Competing Interests

We have no competing interests.

Funding

SM was funded by the Ella and Georg Ehrnrooth Foundation, ICC by the Wissenschaftskolleg zu Berlin.

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Figure and table captions

Table 1. Camouflage types expressed in terms of mechanism, signal and noise. Mechanism defines the camouflage types through their function. Signal identifies the attributes that the different camouflage types affect at various stages of the visual processing pathway. Noise refers to the way in which these attributes' signals are degraded by camouflage. Reference gives examples of studies addressing each camouflage type.

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Row #	Camouflage type	Mechanism	Signal	Noise	References
1	Background matching	Make surface difficult to distinguish from background / minimise edge signal	Surface / 3D shape / form	Background matching colouration across surfaces	[17] [19]
2	Internal disruptive	Add noise to 3D form cues, breaks up surfaces		False correspondences and texture gradients	[36] [40]
3	Background matching	Make edges hard to detect	Edge / 2D shape / silhouette	Background matching colouration at edges	[16] [37] [38]
4	External disruptive	Add noise to / break up edges		Superfluous edges intersecting real edges	[36]
5	Internal disruptive	Distract from edges		Superfluous edges across surface	[40]
6	Disruptive	Lateral inhibition		Superfluous edges in close proximity to real edges	[48]
7	Distraction markings	Distract from edges		Superfluous features away from edges	[46]
8	Eyestripes / co incident disruption	Mask features	Characteristic features	Concealing features	[41] [42]
9	Eyespots / divertive markings	Distract from features		False features	[42]
10	Distraction markings	Divert attention from features		Salient irrelevant features	[43] [44]
11	Disruptive	Interfere with feature binding	Objects	Anti Gestalt	[35] [48]
12	Mimicry / masquerade	Prevent attention / recognition	Motion	Salient false identity signal which is unprofitable to predators	[59] [61]
13	Adapt own motion	Reduce motion signal		Minimise perceived speed	[70]
14	Dazzle	Not well characterised (contrast, size, sampling...)		Distort perceived speed	[75]
15	Dazzle	Aperture effects		Distort perceived direction	[73]
16	Confusion effect	Overload predator attention mechanisms	Individuality	Multiple superfluous signals from non-targets	[78] [79] [82]